T. H. BARRY

THE CRANIAL MORPHOLOGY OF THE PERMO-TRIASSIC ANOMODONT *PRISTERODON BUFFALOENSIS* WITH SPECIAL REFERENCE TO THE NEURAL ENDOCRANIUM AND VISCERAL ARCH SKELETON

December 1967 December

Volume 50 Band

Part 7 Deel

ANNALS OF THE SOUTH AFRICAN MUSEUM

ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

Cape Town Kaapstad

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Verkrygbaar van die Suid-Afrikaanse Museum, Posbus 61, Kaapstad
(Kontant met bestelling, posvry)

OUT OF PRINT/UIT DRUK

1, 2(1, 3, 5, 7–8), 3(1–2, 5, t.–p.i.), 5(2, 5, 7–9),
6(1, t.–p.i.), 7(1, 3), 8, 9(1–2), 10(1–3),
11(1–2, 7, t.–p.i.), 21, 24(2), 31(1–3), 38, 44(4).

Price of this part/Prys van hierdie deel

R1.50

Printed in South Africa by
The Rustica Press, Pty., Ltd.
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.
Courtweg, Wynberg, Kaap

THE CRANIAL MORPHOLOGY OF THE PERMO-TRIASSIC ANOMODONT *PRISTERODON BUFFALOENSIS* WITH SPECIAL REFERENCE TO THE NEURAL ENDOCRANIUM AND VISCERAL ARCH SKELETON

By

T. H. Barry

South African Museum, Cape Town

(With Plates X–XI and 14 figures in the text)

Contents

Summary

The skull of the fossil mammal-like reptile *Pristerodon buffaloensis* has been sectioned and reconstructed to show the external and internal features of the skull. The skull is compared with the type and other specimens as well as with a sectioned specimen of *Dicynodon grimbeeki*.

Special emphasis has been laid on the structure of the neurocranium and visceral arch skeleton. It is suggested that ossified trabeculae are definable in the basicranial axis and that the quadrate and epipterygoid were synchondrotically attached in life to form a palato-quadrate complex.

Ann. S. Afr. Mus. **50** (7), 1967: 131–161, 2 plates, 14 figs.

The stapes is suturally attached to the quadrate, ruling out any movement of the stapes without movement of the quadrate. It is maintained that conditions in *Pristerodon* do not support the theory that anomodonts possessed a tympanum.

Deductions are also made regarding the neck musculature and processes developed on the occiput.

Introduction

Comparative anatomists and palaeontologists have been studying the origin of mammals for more than a hundred years now. At this stage of our knowledge it seems reasonably established that mammals arose from the Therapsids, which in turn arose from the Captorhinomorpha via the Pelycosauria. Most of the research has, quite naturally, been directed at finding the structural links between the mammal-like reptile and the primitive mammal and the tendency has been to study those animals falling within the accepted lines which lead to the mammal.

Side branches are not thought to hold the same fascination as those leading towards the mammals and are often neglected, in spite of the fact that they too can supply a wealth of information regarding evolutionary processes. The Sub-order Anomodontia (Class Reptilia; Sub-class Synapsida; Order Therapsida) is of especial interest not only because it shows a marked degree of parallel evolution of certain mammalian characteristics, but also because the abundance of its species and the availability of specimens make this group ideal for comparative anatomical studies.

According to Haughton and Brink (1954) the characteristics of the genus *Pristerodon* are the following:

> 'Small. Molars situated in a row on the alveolar ridge on the maxilla, postero-medial to the canine or caniniform process. Palatine not in contact with the premaxilla. Parietal bar broad' (p. 65).

The genus is divided into the following species: *Pristerodon agilis*, *P. brachiops*, *P. buffaloensis*, *P. mackayi*, *P. raniceps* and *P. whaitsi*.

Material and Technique

The specimen sectioned, No. B.P.I. 339, was found in 1956 by Mr. J. W. Kitching of the Bernard Price Institute for Palaeontological Research, Johannesburg, on the farm Kirkvors, (today known as De Hoop) approximately 2 miles north-north-west of Murraysburg, South Africa. The horizon is *Cistecephalus*.

The type specimen, No. B.P.I. 241, used in this investigation, is a well-preserved skull (pl. X A, B, C, and XI A, D). It belongs to the Bernard Price Institute for Palaeontological Research. It was found on the farm Swartbos, in the Murraysburg district. The horizon was Lower *Cistecephalus*.

Three other specimens, Nos. B.P.I. 242, B.P.I. 243 and B.P.I. 244, were also used for comparison.

Skull No. B.P.I. 339 was serially sectioned by means of the parallel grinding method, leaving exposed transverse sections at intervals of 200 micron. As it was possible to determine the general outline of the skull the specimen could be orientated for sectioning without removal of the matrix. This had the advantage that clear definition was obtained between matrix and bones and obviated the possibility of accidental grooving or pitting of the bones through mechanical cleaning. Three thin metal rods, fixed parallel to the cranial axis, served as base-lines for the transverse orientation of the skull before imbedding in 'Callistone' plaster of Paris.

In this investigation use was made of a Croft Parallel Grinder. Under normal circumstances the grinding method offers an accurate and satisfactory picture of the relationships of the bones, and supplies information about the internal structures which are not readily available from other methods of

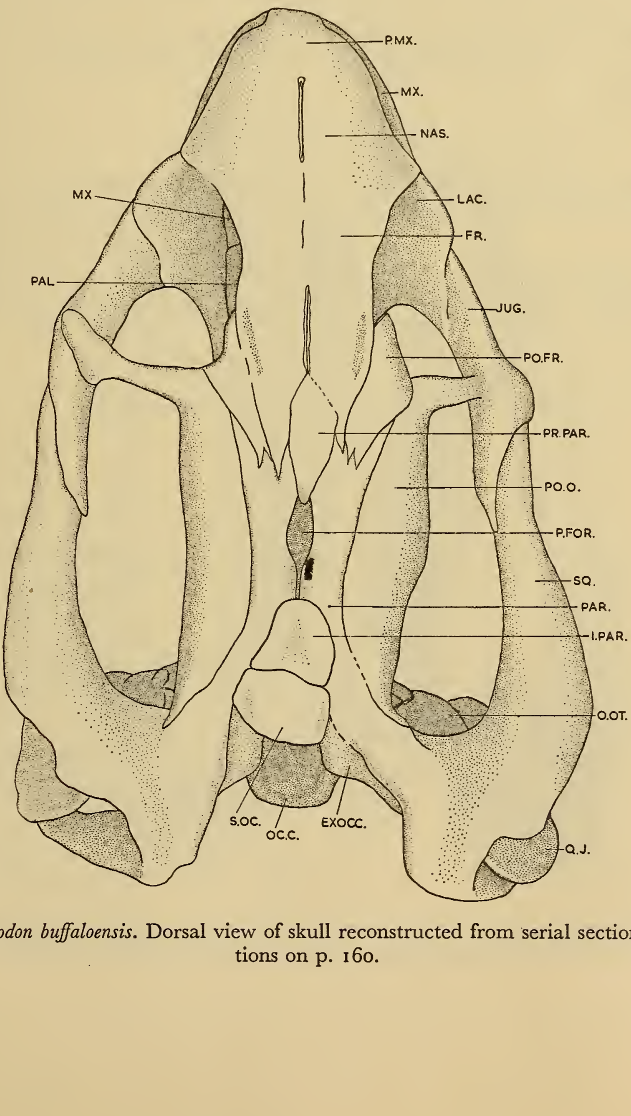

Fig. 1. *Pristerodon buffaloensis.* Dorsal view of skull reconstructed from serial sections. Abbreviations on p. 160.

preparation. The disadvantage of the serial grinding method is the complete loss of the specimen, thus necessitating the use of the more common species in this type of investigation. However, specimens of less common species are sometimes sectioned when the additional information procurable warrants it. Less common specimens are known, however, to have been sectioned in error, in the belief, resulting from the superficial method of fossil identification often employed, that a more common species is being investigated.

To counteract the loss of the fossil, photographs are taken and enlarged drawings made of each exposed surface and these are used later in making the reconstructions. The method used in making the reconstructions is that described by Pusey (1939) for drawings made from microtome sections.

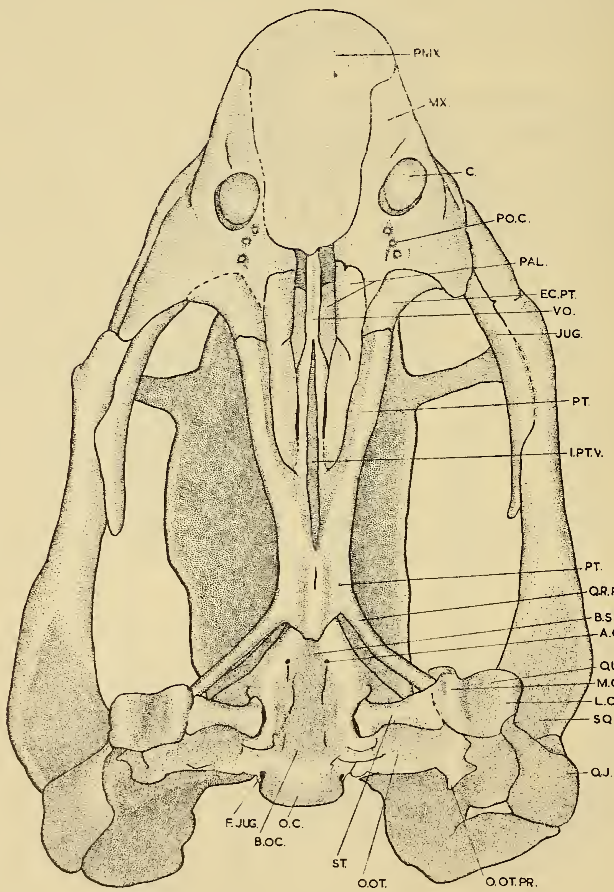

Fig. 2. *Pristerodon buffaloensis*. Ventral view of skull with lower jaw removed. Reconstructed from serial sections. Abbreviations on p. 160.

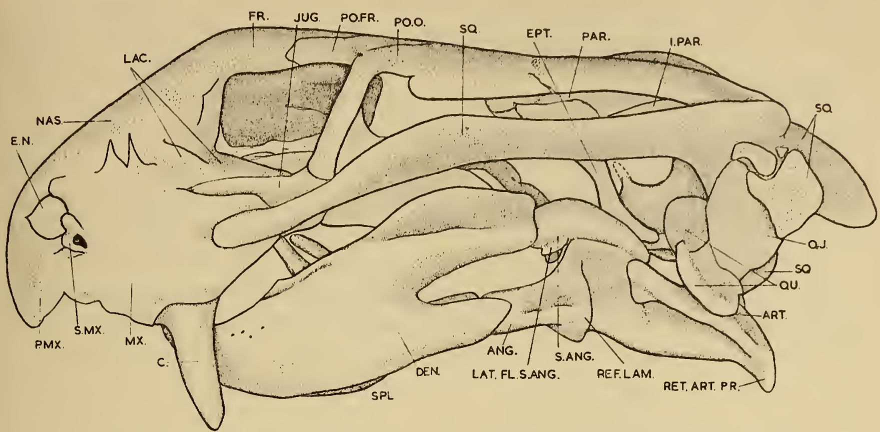

Fig. 3. *Pristerodon buffaloensis.* Lateral view of skull with lower jaw in original position. Reconstructed from serial sections. Abbreviations on p. 160.

Cranial Morphology

Toerien (1953) selected fifteen measurements and indices for a comparative study of skull variation in *Dicynodon grimbeeki* and *D. sollasi.* The same method has been adopted for *Pristerodon buffaloensis.*

The following is a table of the measurements and indices of the sectioned skull and includes a comparison with the type specimen of *P. buffaloensis.*

		Value in mm.	
	Measurement or index	*No.* 339	*Type*
1.	Skull length	64·8	83
2.	Basal length	58·4	76
3.	Skull width	44·8	60
4.	Interorbital width	9·8	13
5.	Intertemporal width	16·2	20
6.	Snout length	16·6	20
7.	Snout length plus orbital length	26·6	40
8.	Tip of snout to pineal length	36·2	49
9.	$\frac{\text{Skull width} \times 100}{\text{Skull length}}$	67·9	72
10.	$\frac{\text{Interorbital width} \times 100}{\text{Intertemporal width}}$	60·5	65
11.	$\frac{\text{Interorbital width} \times 100}{\text{Skull width}}$	21·8	21·7
12.	$\frac{\text{Intertemporal width} \times 100}{\text{Skull width}}$	36·2	33·3

		Value in mm.	
	Measurement or index	*No.* 339	*Type*
13.	$\frac{\text{Snout length} \times 100}{\text{Skull length}}$	18·4	24
14.	$\frac{\text{Snout length plus orbital} \times 100}{\text{Skull length}}$	41·0	48·2
15.	$\frac{\text{Tip of snout to pineal length} \times 100}{\text{Skull length}}$	55·9	59

In Fig. 4 these measurements and indices are plotted against the corresponding ranges of five specimens of *Pristerodon buffaloensis.*

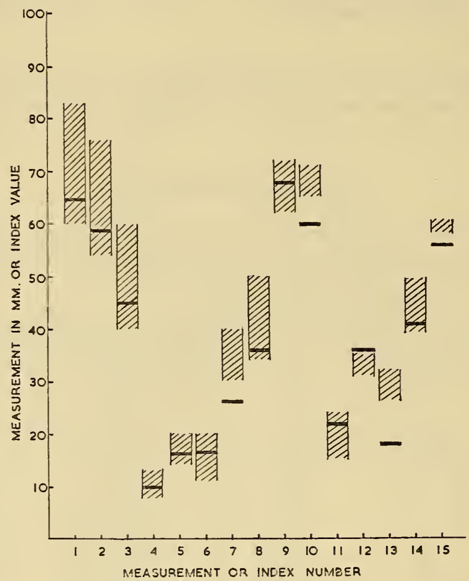

Fig. 4. Range in measurements and index values for five specimens of *Pristerodon buffaloensis.* Ranges indicated by shaded blocks. Values for sectioned specimen by black lines.

Dermal Bones

A feature of the snout region of the sectioned skull is the absence of sutures between the premaxillary, nasal and the frontal bones (see figs. 1 and 3). Transverse sutures are often difficult to distinguish in transverse sections but none of the sutures here should have presented this problem. Of the three specimens of *Pristerodon buffaloensis* figured by Toerien (1953), two do not show sutures between these bones, while in the type specimen the outline of the prefrontal, internasal and nasopremaxillary sutures only are visible. It is possible that the variability of sutures in this region could be the result of suture closure which develops with age, a phenomenon which is not unknown in

extant mammals where various degrees of suture closure have been recorded in older animals. The size of the canine tusks seem to underline the fact that the skull is that of an adult.

The facial portion of the premaxillo-maxillary border is indistinguishable. The palatal portion of the premaxillary is concave and extends to the point in line with the second post-canine tooth, where it forms the anterior border of the internal choanae. Peripherally the bone terminates in a sharp cutting edge. A median ridge developed on the posterior third of the premaxillary projects into the oral cavity. The contact posteriorly between the premaxillary and the median vomer is a deep one involving not only the ventral ridge but also the dorsal ridge which projects into the snout (fig. 5). There is no indication of the pair of shallow palatal ridges found at the anterior end of the premaxillary of *Dicynodon grimbeeki* and many other dicynodonts. Near the midline, in this area the bone is pierced by a small foramen which leads into the nasal passage. Sollas & Sollas (1914) found two pairs of foramina in this vicinity and suggested that these naso-palatine foramina served for the passage of blood-vessels. From the dorsal surface of the palatal portion of the bone, a median plate-like internasal process extends upwards for about one-third of the distance to the roof of the snout. The height of the plate increases posteriorly with the increase in height of the dome of the snout. A shallow groove in the dorsal edge of the posterior half of the plate probably accommodated a cartilaginous nasal septum (see fig. 7A).

No evidence was found that the premaxillaries were paired as reported for *Venjukovia* by Watson (1948). In its front half the bone is pierced by a small foramen.

The degree of progress towards the development of a secondary palate in *Pristerodon* is probably indicated by the increase in relative length of the palatal portion of the premaxillary and the fact that it overlaps a third of the vomer

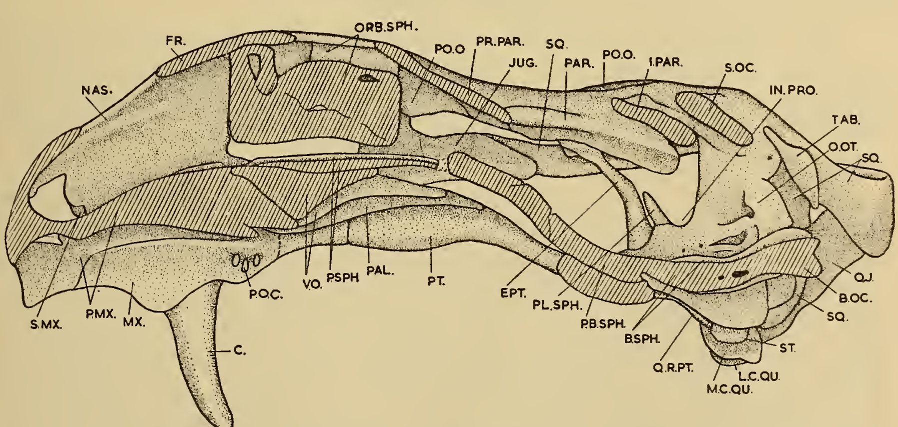

Fig. 5. *Pristerodon buffaloensis*. Medial view of skull of sectioned specimen. Median bones hatched. Abbreviations on p. 160.

behind it. As the median ridge of the premaxillary occupies a position corresponding to that of the anterior part of the vomer in lizards, it is not unreasonable to assume that the ridge on the premaxillary has taken over whatever function was previously performed by the vomer in this area.

The Maxillary

The maxillary forms the major portion of the side wall of the snout projecting ventrally to well below the level of the palate. The sharp peripheral ridge of the premaxillary is continued on to the anterior third of the maxillary before it flattens out on reaching the canine tusk (fig. 2).

Posteromedially the palatal portion of the maxillary participates in the formation of the lateral walls of the choanae through the formation of a wedge which inserts between the premaxillary and the palatine. Toerien (1953) used the relationships between these three bones as basis for the classification of the Anomodontia but this has not been generally accepted.

In addition to the large canine, the maxillary has three small post-canine teeth situated in a row, posteromedially to the canine, and at a slight angle to the longitudinal axis of the skull (fig. 2). The teeth show a slight variation in size, the anterior one being slightly bigger than the other two. The sections do not show whether the teeth were serrated, a feature regarded by Broom as being significant in classification and identification. Toerien (1953), however, claims that serrations only occur on erupting or newly erupted teeth and that the older teeth were completely devoid of denticulations. Nor can the number of post-canine teeth be used as a basis for generic or specific distinction as the number can vary not only within the same species but also on the two sides of the upper jaw. Specimen No. B.P.I. 243, like the sectioned skull, has three post-canine teeth in each half of the upper jaw. The type, however, has four. There are no replacement teeth in the upper jaw of the sectioned skull but the type and B.P.I. 243 show at least one each.

The maxillary antrum is not an intra-osseal maxillary space, as Broom claimed for *Oudenodon*, but inter-osseal, with the maxillary, jugal and lachrymal participating in its formation (fig. 7A). This is also the case in *Daptocephalus* (Sollas & Sollas, 1914), but in this form the transpalatine also contributes to the walls of the cavity.

The median vomer is attached to the premaxillary in front of it over a narrow but extremely deep, posteriorly slanting vertical area. Transverse sections show that the premaxillary is actually continued further posteriorly than is seen from the outside because a thin postero-ventrally directed sliver of the premaxillary is wedged into the vertical vomer so that the latter virtually clasps the posterior part of the premaxillary between two thin laminae. At approximately two-thirds of its length measured from the front, the vomer splits into two flanges, each of which attaches laterally to the palatine and posteriorly to the pterygoid. The flanges demarcate the anterior part of the interpterygoidal vacuity. In median section the vomer shows as a triangular bone with the apex

of the triangle pointing ventrally (fig. 5). From the apex to the point where the vomer splits, the ventral surface is deeply grooved as if it housed a cartilaginous structure (fig. 7C).

The dorsal surface of the plate-like median portion of the vomer is also grooved, housing the anterior portion of the parasphenoid rostrum in a close fit.

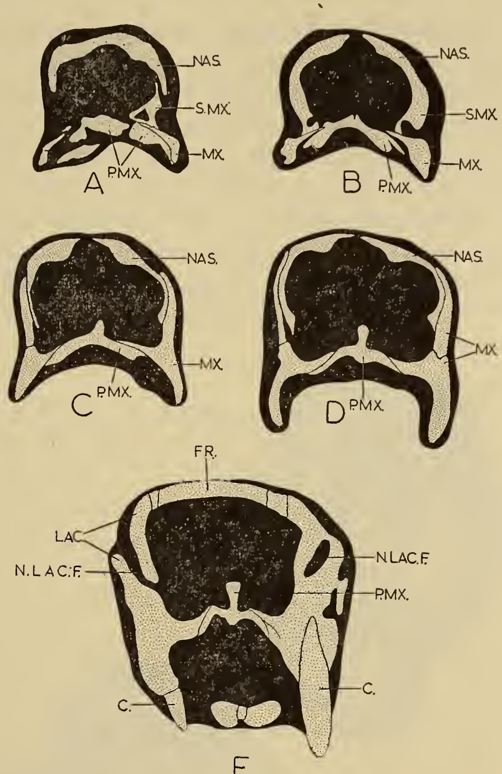

Fig. 6. *Pristerodon buffaloensis.* A–D: transverse sections through the snout of the sectioned specimen. Abbreviations on p. 160.

The Septomaxillary

The septomaxillary, a typically reptilian membrane bone represented in only two orders of mammals, the Monotremata and the Edentata (De Beer, 1937), occupies the postero-ventral border of the external nostril in *Pristerodon.* It is roughly triangular in cross-section with the base resting mainly on the palatal process of the maxillary. As in *Dicynodon grimbeeki*, an obliquely running longitudinal canal pierces the bone. In *Dimetrodon*, the only pelycosaurian species in which the septomaxillary is fully known, a foramen of moderate size pierces the base of the bone near its external border (Romer and Price, 1940). It is possible that the canal served to transmit blood-vessels and

nerves into the nostril, as it still does in the lizards *Cordylus polyzonus* (Van Pletzen, 1946) and *Monopeltis capensis* (Kritzinger, 1946). In these two species the ramus medialis nasi V, accompanied by a small artery, passes through a foramen in the anterior tip of the septomaxillary. In *Anniella pulchra*, however, the blood-vessel and nerve are accommodated in a deep groove on the dorsal surface of the bone (Toerien, 1950).

Williston (1925) claims that the primitive position of the septomaxillary is on the postero-lateral rim of the external naris, a position corresponding to that occupied by the bone in *Pristerodon buffaloensis*. In *Sphenodon* where the septomaxillary occupies a corresponding position, it is solely concerned with the support of the floor of the Organ of Jacobson and with the formation of the side wall of the vestibule (Fuchs, 1911). According to Fuchs the same conditions obtain in *Dasypus*. Whether *Pristerodon* possessed a vomero-nasal organ, which, as in *Sphenodon*, opened into the choana, or whether like adult Chelonians, crocodilians and birds, it lacked one (Romer, 1949) is difficult to say, but there are no separate openings in the palate anterior to the choanae which could be associated with their ducts.

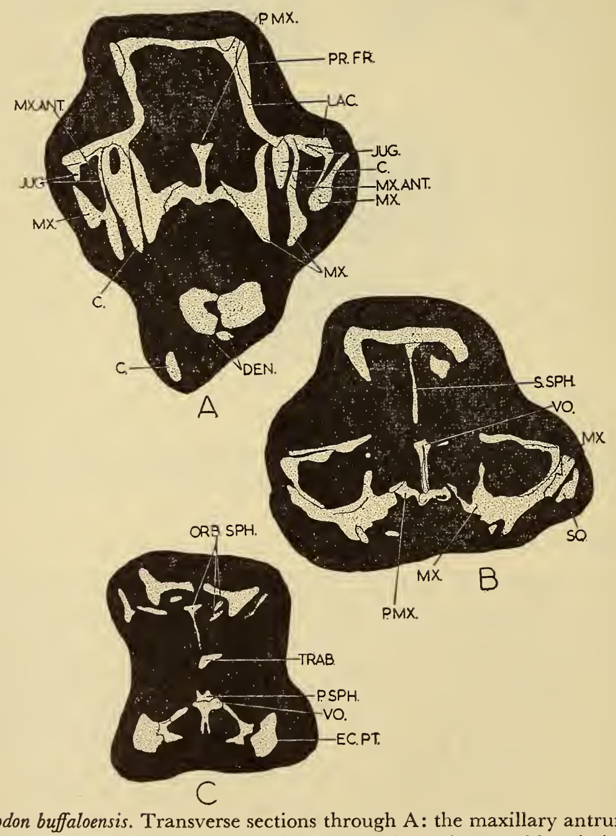

Fig. 7. ***Pristerodon buffaloensis***. Transverse sections through A: the maxillary antrum; B: anterior part, and C: posterior part of the orbit of the sectioned specimen. Abbreviations on p. 160.

The Nasal

The anterolateral tip of the nasal contributes to the formation of the rim of the external naris. The nasal also forms the major portion of the internal dome-shaped nasal cavity, contributing the lateral and dorsal walls. One-third to one-half of the lateral surface of the bone is overlapped by the facial portion of the maxillary (figs. 6C & D).

Cross-sections show a shallow, rounded ridge, high up on the inner surface of the nasal cavity, which extends from the external naris to a point in line with the naso-lachrymal foramen (figs. 5, 6C & D). The ridge is mostly evenly rounded but it may also jut out in the form of a ledge. It is possible that the ridge represents the area of a lateral attachment of a membranous or cartilaginous structure which extended across the dorsal part of the nostril and probably formed the floor of the olfactory lobes. A seemingly comparable ridge on the inner surface of the snout in the lizards *Scelotes* and *Anniella* (Malan, 1946) albeit on the frontal, serves as attachment for the membrane supporting the anterior part of the olfactory lobes.

The Lachrymal

The lachrymal forms the major portion of the anterior rim and floor of the orbit. Anteriorly it expands into the side of the face (fig. 3) but it ends well behind the naris.

Individually, the frontal, postfrontal, preparietal, parietal, interparietal and postorbital show little structural deviation from conditions as seen in *Dicynodon grimbeeki*, but collectively they form a pattern which distinguishes *Pristerodon* from other small-skull anomodonts. Here the relative widths of the interorbital and intertemporal bars, seen within the outline of the skull, are of importance especially as they simplify superficial identification.

A feature which has possibly more significance than would normally be attributed to it, is the rounded depression in the fronto-parietal region. A similar type of depression is seen in the type specimen (pl. XA & C). Although such a condition would normally be attributed to post-mortem damage, the fact that the depression occurs in a small specific area and that it is so neatly excavated makes it difficult to accept, without reservation, that it was caused by pressure from above. It is believed that this area of the skull in *Pristerodon* was either normally depressed or otherwise the flatness of the skull makes it less resistant to pressure than the slightly convex skull of many *Dicynodon* species.

The Squamosal

The squamosal is tetraradiate. Its antero-ventrally directed flange, which with the jugal on its inside, forms the temporal arch, extends forward to contact the maxillary, ventral to the anterior rim of the orbit. Its antero-dorsal process is short and runs medially to the postorbital. The third prong is extended ventrally and gains contact with the quadrato-jugal, quadrate, tabular, exoccipital and opisthotic, while the fourth process is posteriorly directed. It is

probable that the shallowly grooved dorsal surface of this flange, as well as the dorso-medially flattened surface of the squamosal in the temporal arch, are associated with the attachment of the adductor muscles.

The Neurocranium

The Occiput

The interparietal and tabular, both of which are dermal roofing bones, and the squamosal appear on the hind wall of the skull. For the rest the occiput is formed by cartilage bones.

The posterior surface of the supraoccipital is in contact laterally with the tabular and ventro-laterally with the exoccipital. It is the roofing bone of the foramen magnum, and the posterior portion of the brain (pl. XIa & c). The body of the supraoccipital extends forward along the midline to a point in line with the pro-otic incisure. Its ridge-like ventro-lateral border forms a sutural contact with the dorsal portions of the exoccipital and pro-otic.

The exoccipital extends plate-like across the posterior surface of the skull to form the lateral border of the foramen magnum, the medial and ventral borders of the post-temporal fossa and the dorsal half of the rim of the jugular foramen (for nerves IX, X and XI). Dorso-laterally it is bordered by the tabular, laterally by the squamosal, ventro-laterally by the opisthotic and ventro-medially by the basioccipital. Exoccipital participation in the formation of the occipital condyle seems restricted to the lateral bulges of the condyle although the sutures are not very well defined. The exoccipitals do not exclude the basioccipital from the foramen magnum as in *Daptocephalus* (Ewer, 1961) and *Lystrosaurus* (Van Hoepen, 1913).

The post-temporal fossa is small. According to Versluijs (1936) the fossa tends to become smaller in those groups where the surrounding bones become more robust. In *Pristerodon* the dorsal expansion of the opisthotic and the enlargement of the tabular have narrowed the size of the opening and consequently the area of attachment of the temporalis muscle on the occiput has also been decreased. Versluijs (1936) has found that the neck muscles play an important part in the determination of the shape of the hind wall of the skull, while Pointner (1931) maintains that traction not only exerts its influence on the construction of a bone but that the relative length of the functionally important neck muscles can be ascertained from the bones forming the hind part of the skull.

The occiput in *Pristerodon* indicates the origin of at least three groups of neck muscles and two jaw muscles. The rectus capitis posterior group shows signs of subdivision into a large dorsal muscle, the rectus capitis posterior major, having an area of origin occupying the supraoccipital, tabular and the dorsal half of the exoccipital, and the rectus capitis posterior lateralis et medialis occupying most of the ventral and lateral portions of the exoccipital and the dorsal half of the opisthotic (pl. XIc). Contraction of the r.c.p. lateralis et medialis would pull the skull back while the lateralis portion would have some

influence in swinging the snout sideways. The r.c.p. major would also pull the skull back but the forward slant of the hind wall of the skull dorsal to the foramen magnum suggests that its contraction would also lever the snout upwards. This action would allow the animal to tear off portions from its food source which are small enough to be handled by the jaws.

The ventral half of the distal portion of the opisthotic served as origin for the obliquus capitis. Contraction of this muscle which in living reptiles is inserted on the neural arch of the axis and atlas, would cause a lateral swing of the skull. Between this muscle and the lateral portion of the one above it (r.c.p. lateralis et medialis) the opisthotic is drawn out into a pointed posteriorly projecting process, which may be called the opisthotic process for lack of a more suitable name.

Stresses caused by the contraction of these two functionally important but differently directed muscles would seem to be the main reason for the development of the opisthotic process. Cox (1959) contends that this process, which he called the 'tympanic process', was not concerned with the occipital musculature. Comparison of *Pristerodon* with living chelonians gives strong indications that the two muscle groups mentioned not only flanked the process dorso-medially and ventro-medially respectively, but were also attached along part of the process. It is of interest to note that some of the recent turtles show an analagous

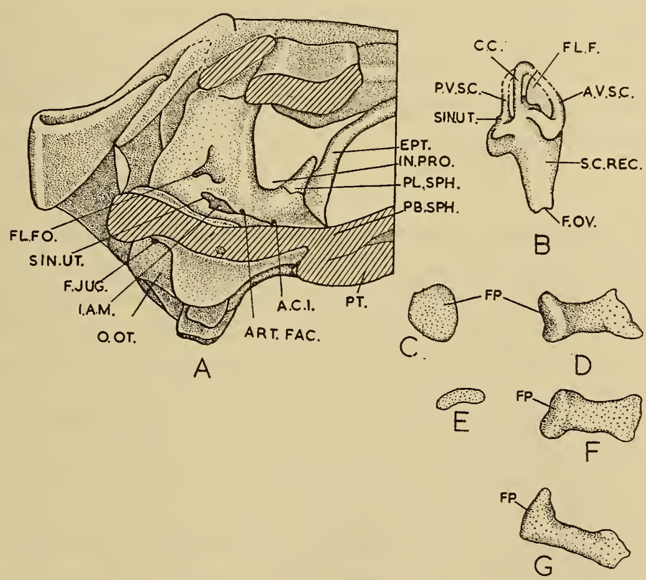

Fig. 8. *Pristerodon buffaloensis.* Sectioned specimen. Reconstructions of A: medial view of posterior third of the skull; B: lateral view of impression of left membranous labyrinth; C: medial view of stapes footplate; D: dorsal view of right stapes; E: lateral view of quadrate face of the right stapes; F: ventral view of right stapes; G: posterior view of right stapes. Abbreviations on p. 160.

process on the opisthotic, more prominently developed in some than in others (pl. XIB). The muscle attachments on one of them, *Pelomedusa subrufa* show the muscles extending along nearly the entire length of the process.

A scar on the inside of the basioccipital-basisphenoid tuber probably indicates the area of attachment of the rectus capitis anterior. In living reptiles this muscle is inserted on the ventral surface of the axis and atlas. Contraction in *Pristerodon* would, therefore, pull the snout down.

The depressor mandibulae is the more prominent of the two jaw muscles associated with the hind wall of the skull in *Pristerodon* and covers the entire surface of the occipital face of the squamosal. A transverse ridge half-way down, similar to that found in most recent turtles, probably demarcates the border between the area of origin of a dorsal longer group, from a ventral, shorter, group of muscle fibres. The depressor is inserted on the ventral posterior part of the lower jaw.

The small post-temporal fossa allows only a small portion of the second jaw muscle, the temporal, to enter the hind wall.

The internal ear

The features of the internal ear are distinct except for small portions of the semi-circular canals which have become obliterated (fig. 8B). The structure of the ear does not seem to differ radically from the anomodonts described by Sollas & Sollas (1914) and Olson (1944). There is no sign of an endolymphatic duct, and only one ampulla, that of the posterior vertical semicircular canal, can be made out. The sacculus ends distally in the fenestra ovalis. The perilymphatic duct would seem to have entered directly into the jugular canal at the level of the sacculo-utricular junction.

The Stapes

In most anomodonts the prominent postero-ventral tubers, which form the bony casing for the fenestra ovalis, are described as being formed by the basioccipitals, but this could not be confirmed in *Pristerodon* because of the lack of well-defined sutures in this area. Between the tuber, proximally and the quadrate, distally the stapes lies at right angles to the cranial axis with a slight ventral inclination laterally. Viewed from the ventral side it is broad and dumbell-shaped; in posterior view it is flat and L-shaped with the footplate forming the dorsal expansion (see figs. 8C–G). The diameter of the footplate is greater than that of the fenestra ovalis with the result that it overlaps it considerably, especially ventrally. The plate presses against the rim of the tuber but is nowhere fused to it. Halfway along the length of the stapes the shank exhibits a slightly raised dorsal edge which might have been the point of attachment of a ligament. There is no stapedial foramen.

The anterior one-fifth of the quadrate facet of the stapes is free from the quadrate but the rest of the bone is suturally attached to the quadrate. This facet is compressed dorso-ventrally to give it a slightly raised, semicircular out-

line. The postero-lateral part of the facet is extended backward as a process and lies against the downwardly directed paroccipital process. The extent of the fusion of the distal end of the stapes and the quadrate rules out lateral movement of the stapes without concomitant movement of the quadrate. This is a point worth considering for, as will be seen later, the quadrate lies free in the groove between the quadratojugal and paroccipital process except for its attachment to the stapes and a short sutural attachment to the base of the quadratojugal.

The presence or absence of a tympanum in Anomodonts is still a subject of controversy with Camp and Welles (1956), Cox (1959) and Ewer (1961) disclaiming Watson's (1953) view that the Anomodonts did not possess a tympanum. The arguments in favour of a tympanum largely hinge around facets and processes on the stapes and grooves on the quadrate which, according to these authors, could indicate the presence in life of an extrastapedial process and, therefore, also a tympanum.

Camp and Welles (1956) believe that a cartilaginous extrastapes was present in the Anomodont *Placerias* and that it extended from the ventro-lateral extremity of the stapes along a groove sometimes found at the back of the quadrate. Suffice it to say here that *Pristerodon* shows no such groove.

In support of his view that *Kingoria* possessed an extrastapes, a tympanum and an external auditory meatus, Cox (1959) points to the presence of a small facet on the postero-lateral corner of the stapes as possibly marking the point of attachment of an extra-stapedial cartilage, and a backwardly directed process on the opisthotic (his 'tympanic process') which according to him could have served as dorsal attachment for the tympanum.

Cox's argument that the opisthotic process (which also occurs in *Pristerodon* and has been described earlier in this paper) was associated with a tympanum and not with muscle attachments must be rejected on the ground that a process similar to it occurs in *Phrynops* and several other recent turtles, where it is surrounded by neck muscles and where its sides are utilized for the attachment of these muscles. The significance of the postero-laterally directed facet on the distal end of the stapes, which he suggests might be for the base of a cartilaginous extrastapes can be discussed in conjunction with Ewer's (1961) claim.

Ewer found a small shaft-like bone lying loose against the right ramus of the lower jaw of *Daptocephalus* of which she states: 'At one end it expands to form a little facet slightly inclined to the axis of the shaft. If this facet is placed against the facet on the distal end of the stapes a good fit is obtained and I believe the little bone to be an ossified extrastapes. If this is correct then its only possible function is to connect the stapes with the tympanum' (p. 391).

Personal examination of Ewer's material provides conclusive evidence that the shaft-like bone she identified as the extrastapes is, in fact, the posterior part of the shorter of the two hyoid bones she found in the same skull. The shaft-like bone and the hyoid fit perfectly and even the colour variations which occur within the core of the two broken ends match perfectly. When the two bones are joined in this way they form a structure which, if placed in the position sug-

gested by Ewer, would extend well past the lateral limits of the quadrate. This feature and the fact that the joined structure is a mirror image of the longer bone which she identified as a hyoid bone, and with which I am in agreement, disclaim her suggestion that the small shaft-like bone represents an extrastapes. If the hyoid bone is fitted to the facet on the stapedial process it shows that it curved backward and downward, resembling to some degree the curvature of the ceratohyal in *Sphenodon*. The claim that the shaft-like bone represents part of a hyoid cornu is strengthened by the discovery that in two species of *Lystrosaurus* the ends of the hyoid bones (identified as the ceratohyals) are fused to the postero-ventro-lateral border of the stapes (Barry, 1967). In an *Oudenodon* investigated by Mr. M. A. Cluver of the South African Museum the posterior process is developed as a medio-laterally compressed process which shows indications of a shallow facet. However in *Pristerodon* and most of the smaller dicynodonts investigated, the facet is only weakly developed. It is clear, therefore, that the different degrees of development of the posterior process on the stapes in Anomodonts are associated, not with an extrastapedial process, but must be credited to a variable association with the hyoid apparatus.

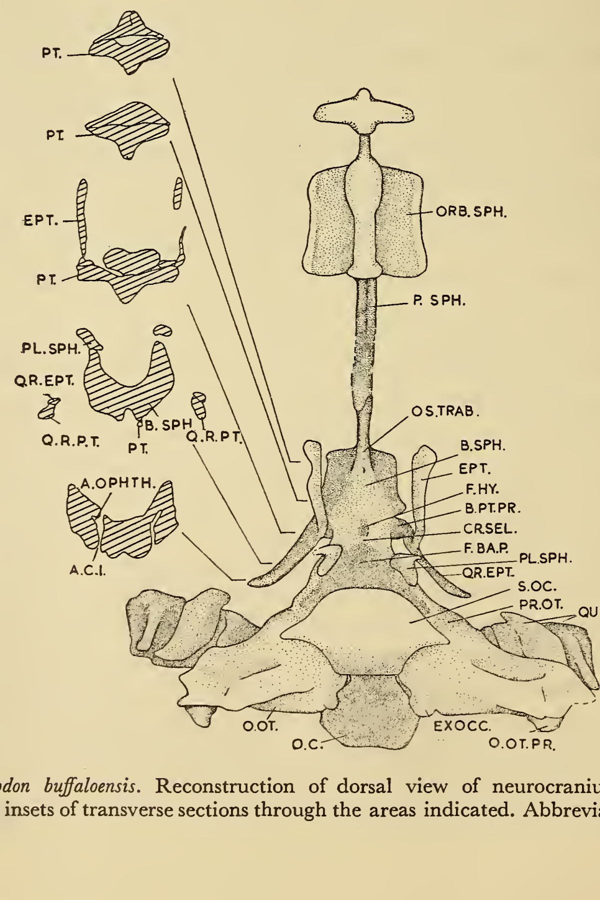

Fig. 9. *Pristerodon buffaloensis*. Reconstruction of dorsal view of neurocranium of sectioned specimen with insets of transverse sections through the areas indicated. Abbreviations on p. 160.

The tubera also form a bony casing for part of the cochlear recess of the internal ear. Two converging ridges extend anteriorly from the tubera to form a deeply excavated area between them. In the type specimen the art.[e] carotis internae pierce the skull at the confluence of these ridges (pl. XB) but in the sectioned specimen they pierce the ridges much further back. Within the bone each artery gives off a branch possibly representing the art. ophthalmica (fig. 9).

Immediately in front of the confluence, the floor of the brain case widens to form a flat, roughly rectangular structure (figs. 9, 10). Near its posterior border the sides of this rectangle are notched, thereby separating it from the two posterior processes. It is suggested that the rectangular base represents the lateral wings of the parasphenoid and the two processes, the pterygoid processes. The identification of the latter are based on the fact that the antero-ventral borders of the epipterygoids are in sutural contact with the processes.

On top of the parasphenoid wings there is a dorsally rounded to flattened triangular raised area which, it is suggested, represents the ossified trabeculae. The apex of the triangle, which points anteriorly, represents the trabeculae communis, the posteriorly widening area of the triangle representing the diverging trabeculae cranii (fig. 9). Between the separated trabeculae there is a shallow depression which probably represents the hypophysial plate. The depression is terminated posteriorly by a rounded transverse ridge which probably represents the ossified dorsum sellae. Behind the latter the base is again depressed. This area probably represents the filled in fenestra basicranialis posterior. A median basicranial fontanella is found further back.

Anterior to the parasphenoid wings, the parabasisphenoid complex is continued as a narrow, relatively high, rostrum which gradually curves upwards towards the interorbital septum where it becomes shallower and straightens out horizontally. It is probable that the trabecula communis extends anteriorly beyond the apex of the triangle and forms at least the dorsal part of this rostrum. There are questionable indications of a suture dividing the rostrum horizontally along its length and the shape of the posterior part of the rostrum lends support to the conclusion that it consists of two fused elements; the rostrum parasphenoidale ventrally and either a rostrum basisphenoidale or a rostrum praesphenoidale dorsally (see fig. 5). The latter depends upon whether the ossification in the travecula communis represents an extension anteriorly into the trabeculae of the ossification of the basisphenoid or whether it is a separate ossification in the trabecula communis.

Among recent reptiles, lizards display a rostrum parasphenoidale while *Chelone* has a rostrum basisphenoidale (Fuchs, 1910; Nick, 1912: quoted Versluijs 1936). In crocodiles the basisphenoid ossification extends forward into the travecula communis to just behind the optic chiasma (Bellairs, 1949).

At the point where the upwardly curved rostrum straightens horizontally, there is a short break in the bone and it is assumed that participation of the

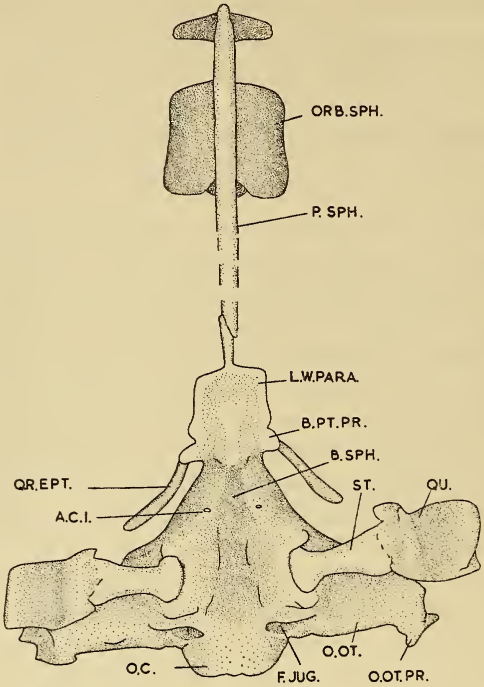

Fig. 10. *Pristerodon buffaloensis.* Reconstruction of ventral view of neurocranium of sectioned specimen. Abbreviations on p. 160.

presphenoid in the formation of the rostrum must have ended in this region, as the structure of the rostrum anterior to the break is distinctly different. It is reduced to about half its previous height and a longitudinal dorsal groove now runs along its length (fig. 5). This section of the rostrum is probably of parasphenoid origin, an extension anteriorly of the ventral portion of the parasphenoid-presphenoid rostrum. The front half of the rostrum lies in a shallow groove in the dorsal edge of the vomer. Anterior to the front end of the rostrum the dorsal groove is continued forward in the vomer and premaxilla. As this portion of the groove and that in the rostrum parasphenoidale behind it lie in a straight line and on a horizontal plane, it would seem to indicate a sliding action which was either used by the living animal or merely represents the retention of an ancestrally functional apparatus. Contact between the rostroparasphenoid and vomer is such that movement between these bones would not be possible—a point of importance in the evaluation of kinetism in *Pristerodon.*

The anterior part of the neurocranium is of especial interest in anomodonts as the '. . . principal problems of evolution of the sphenethmoid complex are to be found in the transition from therapsids to mammals'. (Olson, 1944: 77.) Unfortunately the derivation of the structures forming the bony complex in

anomodonts has not been fully agreed upon with the result that a terminology has arisen which instead of clarifying the position, has complicated it. Seeley (1898) considered the entire complex to be the orbitosphenoid; Sollas & Sollas (1914, 1916) called it the mesethmoid; Broom (1926) stated that it was the presphenoid; Olson (1944) subdivided the complex into a dorsal orbitosphenoid with a possible mesethmoid component, and a ventral presphenoid, while Camp (1956) used the term septosphenoid and frontosphenoids where separate lateral wings occur.

In *Pristerodon* the complex consists of a median bony interorbital plate roughly rectangular in shape and extending from the anterior rim of the orbit to the postorbital bar; paired, trough-shaped projections from the dorsal ridge of this plate and paired rod-shaped projections on the antero-ventral borders of the pro-otics. A study of the sections shows a break in the interorbital plate which runs from antero-dorsal to postero-postero-ventral. The two triangular bones thus formed may well represent anterior and posterior ossifications within the cartilaginous septum of the living animal.

As the posterior ossification includes the dorso-lateral expansions of the interorbital septum, representing the planum supraseptale of recent reptiles, and the planum and most of the interorbital septum in gnathostomes develop from the orbital cartilages (De Beer, 1926; Shaner, 1926), it is reasonable to assume that the posterior triangle represents an orbitosphenoid. In *Lacertilia* the orbitosphenoid is normally limited to the pila metoptica but in *Iguana* Bellairs (1949b) and *Monopeltis* (Malan, 1946) the orbitosphenoid ossification extends into the planum supraseptale and the dorsal part of the interorbital septum. In *Monopeltis* it invades even the posterodorsal part of the nasal septum.

The anterior ossification is definitely a separate ossification but it is difficult to ascertain to what extent the trabeculae contributed to its formation. If the ventral rim of the anterior ossification is divided into quarters it will be seen that the anterior quarter shows no thickening of the rim, the second quarter shows a concave ventral rim, while the third and fourth quarters display a ridge which becomes progressively thicker and even round in cross-section. There would, therefore, seem to be some justification for the assumption that the trabeculae are incorporated into the posterior half of the ventral periphery but that it remained cartilaginous farther forward and fitted into the concave ventral groove mentioned earlier. The gap between the interorbital plate and the rostrum parasphenoidale below it, is probably due to a displacement dorsally of the former. In the older literature any ossification in the interorbital septum of lizards was called a presphenoid (Huxley, 1863; Parker, 1880, etc.) but as Camp (1942) and Bellairs (1949a) have pointed out this is undesirable since the term has been more generally used for the trabecular ossification which develops in contact with the basisphenoid. The term septosphenoid, suggested by Camp (1942) would, therefore, be more suitable. The anterior portion of the septosphenoid reaches the roof of the orbit where it expands laterally to form two narrow, slightly convex, wings (figs. 5, 9, 10).

These projections probably covered the olfactory lobes from above and could conceivably represent the commissurae sphenethmoidalis of recent reptiles. Slightly farther back the wings of the orbitosphenoid project outward and upward from the dorsal rim of the septum. They occupy the position of the planum supraseptale of recent reptiles and should probably be regarded as such. The continuation of the parasphenoidal groove beyond the anterior limit of the septosphenoid indicates that the interorbital septum was probably extended farther forward in cartilage. It would also seem probable that the nasal cavity had some form of median division, as the floor of the premaxillary in this region displays a remarkably well-developed dorsally directed longitudinal ridge, which occupies a position in line with the parasphenoid rostrum behind it (figs. 6B, C, D & E). The grooved dorsal aspect of this ridge, shown in many sections, and the low, longitudinal ridges high up on the inner surface of the nasal cavity, described earlier as possibly representing dorso-lateral projections of a median nasal septum would seem to strengthen this view.

The pleurosphenoid forms the hindmost element of the side wall. It is an antero-dorsally directed, rod-shaped process, internally attached to the basisphenoid (figs. 5, 8, 9 & 12A).

The Visceral Arch Skeleton

The Palatoquadrate

The palatoquadrate of *Pristerodon* is represented by two separated bones, the epipterygoid and the quadrate. Viewed laterally the epipterygoid is L-shaped with both the vertical limb and the posteriorly directed horizontal limb well developed. The vertical limb is relatively thin and extends upwards and slightly forwards towards a ventrally directed lamina extending from the ventral surface of the parietal.

The epipterygoid is widest near the angle of the bone and here it is connected to the basisphenoid by a short basipterygoid process (figs. 11, 12A & B). The entire base is applied to the dorsal and/or dorso-lateral surface of the quadrate ramus of the pterygoid which is directed towards the inner surface of the quadrate.

The quadrate lies in a deep concave groove between the squamosal and the paroccipital. Except for short sutural attachments to the base of the quadratojugal postero-laterally and the distal head of the stapes medially, the quadrate lies free in the groove. In life it probably had a cartilaginous head.

In cross-section the quadrate is shaped like an inverted Y, the two ventrally directed limbs representing the medial and lateral condyles. These are separated by a deep groove, which is also utilized as an articular surface. The condyles, which extend the entire length of the ventral face of the quadrates, show that only very limited sideways movement of the lower jaw is possible, a feature also borne out by the close fit of the lower jaw between the upper jaw canines when the jaws are closed. In *Pristerodon*, as in all known Anomodonts,

the lower jaw slides forwards and backwards during mastication. During maximum gape the posterior portion of the articular surface of the articular is involved, but with the close of the mouth and backward traction by the jaw-closing muscles, the jaw slides backwards so that the anterior portion of the articulatory surface is involved when the jaw is closed. This action allows the animal to chop the food. It is interesting to note that in *Endothiodon*, a genus characterized by the loss of canine teeth, Watson (1948) found '. . . the very remarkable condition of a convex articular surface of the quadrate articulating with a convex surface of the articular' (p. 848). Watson maintains that this arrangement permits very free movements as the lower jaw cannot only move forwards and backwards but it is even probable that the jaw can be slewed round on the palate.

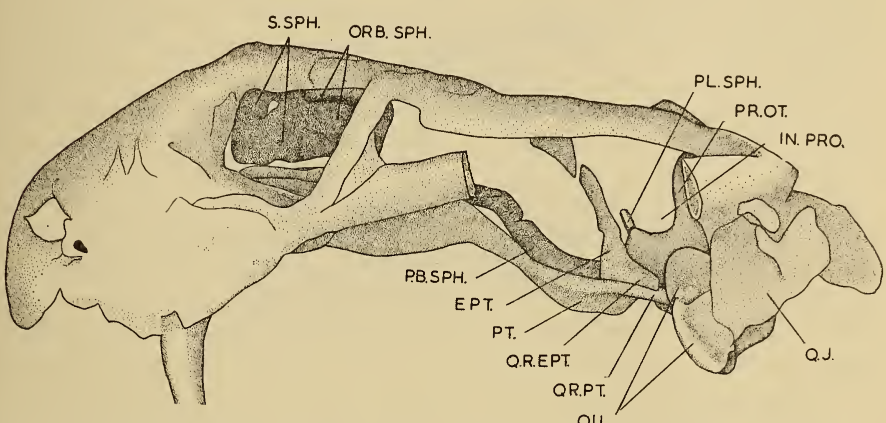

Fig. 11. *Pristerodon buffaloensis.* Reconstruction of lateral view of skull with squamosal cut away to show palatoquadrate complex. Abbreviations on p. 160.

The inner condyle bears a short medially projecting ridge, the stapedial process of the quadrate, to which the distal portion of the stapes is suturally attached. Dorso-medially to this ridge there is a shallow longitudinal groove in the vertical face of the quadrate, extending from the anterior border backwards for approximately one-third of the length of the vertical plate (fig. 12B). Throughout its length this groove is seen to follow remarkably closely a course dorso-laterally and parallel to that of the posterior portion of the quadrate ramus of the pterygoid, the latter bone terminating close to, but free from the inner surface of the quadrate (fig. 12C–E). As the groove follows what could have been the course of a posterior extension of the base of the epipterygoid, it would seem reasonable to assume that the groove contained a rod-like cartilaginous structure connecting the quadrate with the epipterygoid. In the left quadrate a distinct rounded bulge terminates the groove.

As thus reconstructed the palatoquadrate complex of *Pristerodon*, not only shows a remarkable resemblance to the palatoquadrate complex of a 15.2 mm

developmental stage of the Egyptian lizard *Tropiocolotes tripolitanus*, described by Kamal (1960), but the possible occurrence of a solid link between the quadrate and epipterygoid in what is most definitely an adult *Pristerodon*, recalls conditions found in the developmental stages of most recent reptiles and also in the adult *Sphenodon*. The relationship of the base of the complex and the quadrate ramus of the pterygoid in *Pristerodon* and *Sphenodon* fully support these conclusions as the base of the palatoquadrate cartilage always seems to occupy a position on the dorsal and dorso-lateral surface of the quadrate ramus of the pterygoid. The retention of a palatoquadrate complex displaying a link between the epipterygoid and quadrate portions of the complex must then, according to the foregoing remarks, reflect a primary condition. This view is contrary to that expressed by Olson (1944).

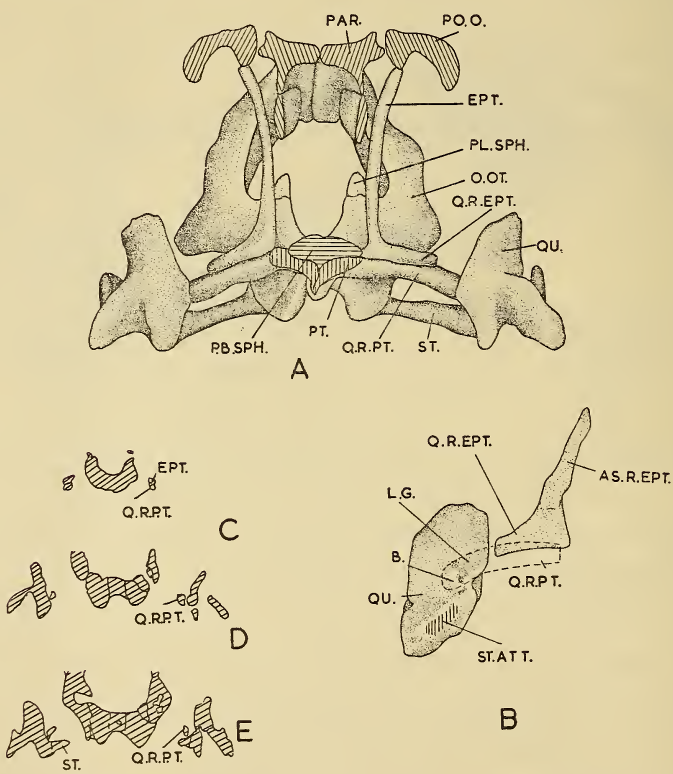

Fig. 12. *Pristerodon buffaloensis*. A: reconstruction of anterior view of palatoquadrate complex; B: reconstruction of medial view of left palatoquadrate complex; C–E: transverse sections through palatoquadrate complex. Abbreviations on p. 160.

In his discussion of the principal changes undergone by the epipterygoid from the primitive reptilian condition to that of mammals, Olson states: 'In primitive reptiles the bone is composed of a restricted basal portion and a

slender ascending ramus, the columella cranii. In somewhat more advanced forms, the basal portion is expanded into a posterior quadrate ramus and an anterior pterygoid process. At this stage the ascending ramus remains a thin rod. In the advanced mammal-like reptiles the ascending ramus is much expanded and has attained intimate association with the periotic behind and the parietal above. The quadrate and pterygoid processes are somewhat elongated' (p. 110).

Phylogenetic and ontogenetic evidence do not lend support to the view that the epipterygoid in the primitive forms possessed a restricted base and the adult forms of recent reptiles bear this out.

As has been shown previously (Barry, 1965) conditions found in recent and fossil forms indicate that the palatoquadrate undergoes divergence in the development of its component parts after the early crossopterygian stage. Those groups leading to or showing affinities with recent reptiles show progressive reduction of that part of the palatoquadrate anterior to the quadrate, while groups with mammalian affinities show reduction of the quadrate. In recent reptiles the quadrate has remained as a fairly strong element but anterior to it only a thin rod-like epipterygoid is left of this part of the palatoquadrate. This is the position in adult forms of many lizards. In others such as *Agama*, *Lyriocephalus* and *Calotes* (Ramiswami, 1966). *Ophioceps* and *Anniella* (Jollie, 1960) further reduction of the epipterygoid has taken place resulting in an epipterygoid which is very short. The epipterygoid is still present but very small in Chelonia (Parker, 1880) while it is much reduced or vestigial in Ophidia and Crocodilia. In Chamaeleontidae, Dibamidae (Boulenger, 1887) and most Amphisbaenidae (known only in Trogonophis, Bellairs, 1950) reduction has been taken further and the epipterygoid has disappeared.

In groups showing mammalian affinities the vertical limb and the base were retained and the former probably expanded while the quadrate has been much reduced and is generally believed to have developed into the incus of the middle ear.

Although the therapsids, as a group, show a marked degree of variability in the structure of the epipterygoid we find that those species which show mammalian affinities invariably show that certain basic features of the complex, represented already in the early gnathostomes and tetrapods, have been retained, with but slight changes, right through to the mammal stage. The most noticeable of these features is the retention of an extensive base to the epipterygoid.

Meckel's Cartilage

In recent reptiles the articular is the only ossification in Meckel's cartilage. Gaupp (1906) mentions that he found a calcification in the anterior end of Meckel's cartilage in an adult *Lacerta vivipara* and that because of this it could not be excluded 'dasz auch bei Sauriern das vorderste Ende des M. Knorpels verknöchern kann' (p. 775). The articular is, however, also the only ossification

in Meckel's cartilage in *Pristerodon*. It displays an articular area which covers more than half of its dorsal length and shows three distinct articular surfaces; a high central articular ridge flanked on each side by a more ventrally situated articular groove (fig. 13A). The medial groove is deeper and shorter than the lateral groove and is situated in a dorso-medially directed flange extending from the centre of the medial surface of the posterior portion of the articular. This flange flares out anteriorly, simultaneously becoming thinner to form a concave plate-like bone. The lateral groove lies in a well-developed lateral projection of the dorsal portion of the articular. This projection extends virtually the entire length of the articular. Anteriorly it is fused to the lateral surface of the surangular, just below the dorsal ridge of the latter. The medial and lateral quadrate condyles fit into these grooves while the articular ridge fits into a corresponding but shorter groove in the quadrate. Among recent reptiles conditions approximating these are only found in the Chelonia.

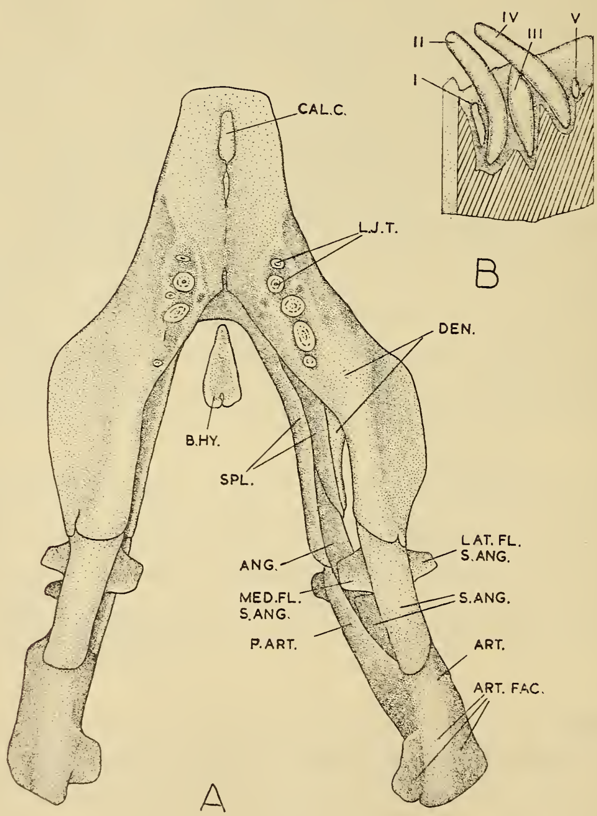

Fig. 13. *Pristerodon buffaloensis*. Sectioned specimen. A: reconstruction of dorsal view of lower jaw with protruding teeth cut off; B: reconstruction of section through right half of lower jaw to show teeth. Abbreviations on p. 160.

The ventral portion of the articular is continued forward as a blunt process covered laterally and ventrally by the angular and medially by the prearticular (fig. 14A). The blunt front end is directed into the meckelian groove. For virtually its entire length Meckel's cartilage lay in a U-shaped groove formed by the prearticular, angular, splenial and dentary (fig. 14B). At the symphysis of the dentaries the groove is continued forward as a canal which pierces the dentary for a short distance before turning medially to meet its mate of the other side. In all recent reptiles investigated Meckel's cartilage lie ventral and ventromedial to the dentary and never pierces it.

There is only a short retroarticular process in *Pristerodon* which is formed as a posterior extension of the central stem of the articular and not, as in *Kingoria*, by the lateral condyle (Cox, 1959). It is not curved ventrally to the same extent as in *Kannemeyeria*, *Stahleckeria* (Camp & Welles, 1956), *Kingoria* (Cox, 1959) or *Emydochampsa* (Broili & Schreuder, 1936, after Jannensch). In *Stahleckeria* and *Emydochampsa* the process actually points downwards and forwards.

Jannensch (1952) states that a horizontally directed retroarticular process is never developed in the anomodonts and that the ventrally directed process found in this group is not morphologically identical with a true retroarticular process. He states, furthermore, that the two processes do not have the same function for, whereas the horizontally directed retroarticular serves for the insertion of the M. depressor mandibulae, the anomodont process could not have had this function, '. . . da von ihm aus eine einigermaszed geradlinige, für Hinterhauptfläche, an der Gelenkkapsel des Kiefergelenks vorbei nicht möglich war' (p. 238).

In reptiles the retroarticular process is absent or only weakly developed in certain Cotylosauria (*Labidosaurus* Versluijs, 1936) some Chelonia (*Emydura*, *Chalydra*, Versluijs, 1936) some Chamaeleontidae (*Peltosaurus*, *Ophioseps* McDowell & Bogert, 1954) and *Amphisbaena* (Versluijs, 1936; Jollie, 1962) but in the majority it is a strong, horizontally developed process serving mainly for the insertion of the M. depressor mandibulae, the main jaw opener in reptiles. The development, or reduction, of the retroarticular process could, therefore, have an effect not only on the insertion of the muscle but possibly also on its development and relationship to neighbouring structures.

In *Pristerodon* structural conditions in the jaws and occiput strongly suggest that the feeding mechanism of this animal resembled that of some recent chelonians. As function plays an important role in muscle arrangement and expression, it would seem logical, therefore, to compare the muscle impressions in the *Pristerodon* skull with the muscular arrangements in those Chelonia which show similarities in the structure of the jaws and occiput. In the latter the M. depressor mandibulae arises from the occipital region of the skull and passes downward to insert on the retroarticular process. The fact that the M. depressor mandibulae is present and functions effectively whether the retroarticular process is large, small or stunted, leaves little doubt that *Pristero-*

don possessed a well-developed and functional depressor mandibulae in spite of the weak development of its retroarticular process (see fig. 14A & B). It is also significant that in spite of the strong development of the M. depressor mandibulae in *Phrynops* and some other Chelonians, the retroarticular process is hardly developed at all. This would seem to weaken Jannensch's (1952) theory.

Hyobranchial Skeleton

In the sectioned skull an independent bone was found lying in the angle of the jaw. Viewed from dorsally the bone is roughly triangular, the apex pointing towards the symphysis of the lower jaw (fig. 13A). There is a shallow medial groove on the dorsal surface which widens posteriorly and then splits when two short rod-like extensions develop.

It is probable that the median element represents the basihyal. If this is so the two short posterior extensions could represent processes for the attachment of cartilaginous ceratogranchials II and the apex, the processus lingualis. In *Sphenodon* ceratobranchials II are fused to the cartilaginous processus lingualis while perichondral ossification can apparently occur in the processus lingualis (De Beer, 1937).

The only known records of ossified parts of the hyoid skeleton in Anomodonts are *Ondenodon*, in which Owen (1859) found a 'uro-hyal', a 'basibranchial' and two 'hypobranchials'; in *Kingoria* where Cox (1959) found a pair of slender rods lying between the rami of the lower jaw and which he believes to be preserved portions of the hyoid skeleton; in *Daptocephalus* in which Ewer (1961) found two branchial horns and a median plate; and in three specimens of *Lystrosaurus* in which the author (Barry, 1967) found ossified ceratohyals.

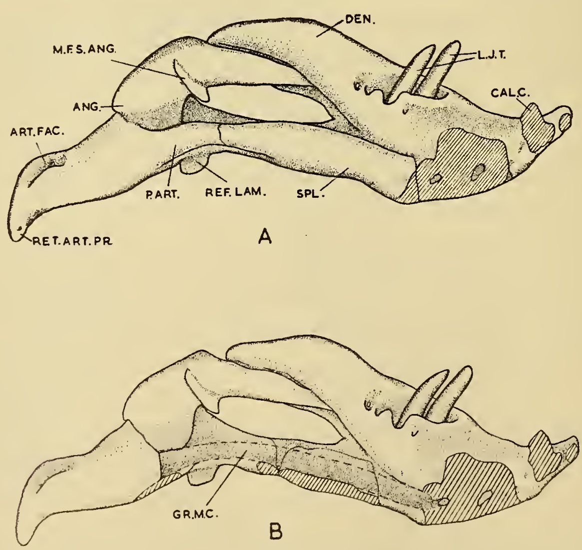

Fig. 14. *Pristerodon buffaloensis*. A: reconstruction of medial view of left half of lower jaw; B: same with bones cut away to show groove for Meckel's cartilage. Abbreviations on p. 160.

Dermal Bones of the Lower Jaw

The lower jaw consists of one cartilage bone, the articular, and five dermal bones, the dentary, angular, surangular, splenial and prearticular. The prearticular, which is indistinguishably fused with the articular, and the splenial form the inner surface of the jaw, while the others are primarily associated with the outer surface (see fig. 14A).

The dentary forms more than half of the lower jaw. The mandibular teeth are arranged in a groove in the dentary which shows indentations corresponding to the roots of the teeth. Viewed superficially the sectioned specimen shows two functional teeth and two empty sockets in each mandibular tooth row (see fig. 13A). In addition two teeth are not in line with the others, but occupy separate sockets medial and lateral to the tooth row in the area of the second and third tooth. In the right half of the jaw both these teeth are missing; in the left half the small lateral tooth is in position. However, as will be seen in figure 13B representing a longitudinal section through the tooth row of the right half, there are unreputed teeth in the groove.

The first tooth is thin and relatively long and in time would have probably replaced the tooth behind it. The latter, which is the first functional tooth but second in the row, is extremely large for the lower jaw. In fact, both functional teeth in the lower jaw are more like lower jaw tusks, being nearly half the size of upper jaw tusks (fig. 3). The third tooth in the right half of the lower jaw is again an unerupted replacement tooth and pushes against the second functional tooth (no. 4 in the row) behind. The fifth tooth in the row is appreciably smaller than any of the preceding ones and it is difficult, therefore, to say whether it will develop into a tusk-sized tooth or whether it will be smaller as is often found in anomodont tooth rows. The medial and lateral teeth behind tooth no. 2 must of necessity remain small and insignificant as there is no room for development. In the left half of the jaw the socket for tooth no. 4 is empty and tooth no. 3 has attained the size of no. 2 in that row and has become functional. There is no tooth bud in the empty socket of no. 4 and we do not, therefore, know if the teeth were replaced more than once.

In the type skull, of which only the left lower jaw was available for study, it was not possible to see the small lateral and medial teeth but the tooth row, apart from showing two additional teeth well back in the row, resembles that of the sectioned specimen. Here, nos. 2 and 4 are long and stout, while nos. 1, 3 and 5 are still developing. Behind tooth no. 5, which is appreciably longer than nos. 1 and 3, there is an empty socket where tooth no. 6 has probably been replaced. Behind position 6 there are three further tooth buds in the row lying in an upward sweep of the jaw. These teeth point forward at an angle of approximately 45° to the horizontal instead of upwards. These teeth probably move forward and rotate upward during life otherwise they would be of little use to the animal. Judging by the size and positioning of the replacement teeth in *Pristerodon* it is almost certain that the teeth were replaced alternately, nos. 1, 3 and 5 replacing 2, 4 and 6.

It is generally accepted that Anomodonts possessed a horny beak. From a functional point of view it would seem reasonable, therefore, to assume that functional teeth would be a limiting factor in the extent to which the boney beak is allowed to overgrow the jaws. If this is the case the horny beak of the upper jaw could not have progressed beyond the canine tusk as the latter as well as the four post-canine teeth situated postero-medially to it would have been the limiting factors. The same considerations would limit the horny beak of the lower jaw to the area anterior to the tooth row. There is a possibility that horn could have progressed farther backwards laterally to the tooth row and on to a shallow longitudinal groove situated here, but this is uncertain.

The longitudinal groove is terminated laterally to the 4th tooth when the dentary arches upward in the form of a crest (see fig. 3). Lateral to this crest the dentary is expanded into a flat-topped ledge probably associated with the insertion of the M. adductor mandibulae externus (possibly the M.add.mand. ext.superficialis). Contraction of this muscle would probably result in retraction of the jaw as the muscle most likely originated on the postero-dorsal flange of the squamosal.

Posteriorly the dentary is bifurcate. The dorsal process overlaps and covers the dorsal and lateral surfaces of most of the anterior half of the surangular while the ventral process overlaps the anterior portion of the angular laterally. The dorsal and ventral arms of the dentary and the angular and the surangular form between them the borders of a relatively large fossa in the lower jaw. This fossa seems to be confined to the anomodonts within the Therapsida but even in this group its development is varied. In *Pristerodon* (see figs. 3, 14A & B) as in *Synostocephalus* (Watson, 1948) the fossa is extremely long, being approximately one-quarter of the length of the lower jaw, while in *Lystrosaurus* it is much smaller. This suggests that soft tissue filling the cavity restricted the dorso-ventral expansion of the dentary flanges but allowed them to continue posteriorly above and below it. If this is the case, it would seem probable that the structure has its origin on the inside of the lower jaw and expanded outwards to a varying degree, depending on its size.

Viewed laterally, the surangular is seen to follow the dorsal arm of the dentary, dipping ventrally towards its end. However, when viewed medially, it is seen that the bone also has a long anterior projection lying in a notch on the medial surface of the dorsal arm of the dentary, while a wide, flat flange lying against and on the inside of the dorsal projection of the angular projects ventrally from the dorsal ridge. Immediately posterior to the dentary the dorsal ridge of the surangular displays two flat ledges, one projecting from the medial (figs. 13A, 14A & B) and the other from the lateral side of the bone (figs. 3, 13A). Both ledges are directed postero-dorsally, the ledge on the inside of the surangular being longer and extending upwards nearly to the top of the surangular. The ledges seem either to have protected some underlying structure in the posterior portion of the mandibular fossa or to have separated it from overlying structures, or both.

The angular which forms a continuation of the ventral arm of the dentary is trough-shaped forming the medial and lateral wall of the groove which housed Meckel's cartilage. The reflected lamina of the angular is funnel-shaped with the opening facing posteriorly (fig. 3).

Acknowledgements

I wish to record my indebtedness to the South African Council for Scientific and Industrial Research for the allocation of research and capital grants to conduct this investigation. My thanks are also due to Dr. A. S. Brink of the Bernard Price Institute for Palaeontological Research, Johannesburg, for permission to section the specimen used in this investigation, and for the loan of the type and other specimens. To Dr. M. E. Malan of the Zoology Department of the University of Stellenbosch my thanks for her critical reading of the manuscript of this paper.

The Trustees of the South African Museum are grateful to the Council for Scientific and Industrial Research for a grant to publish this paper.

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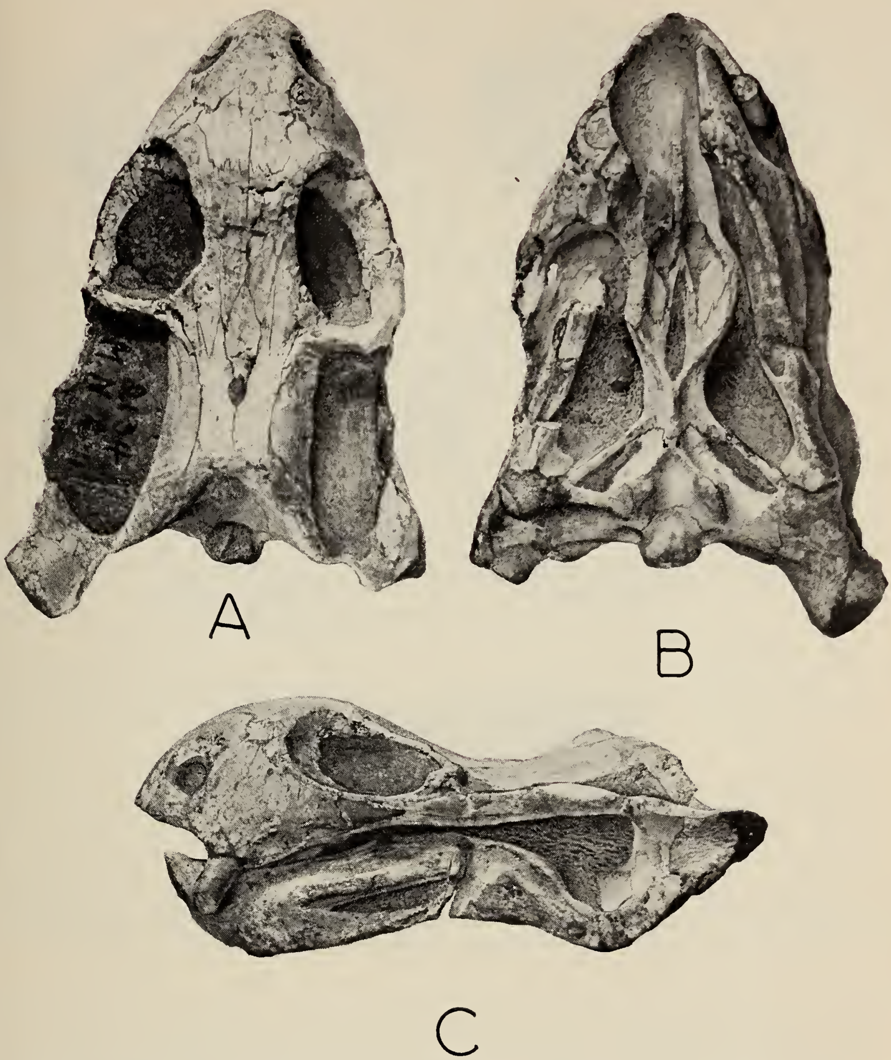
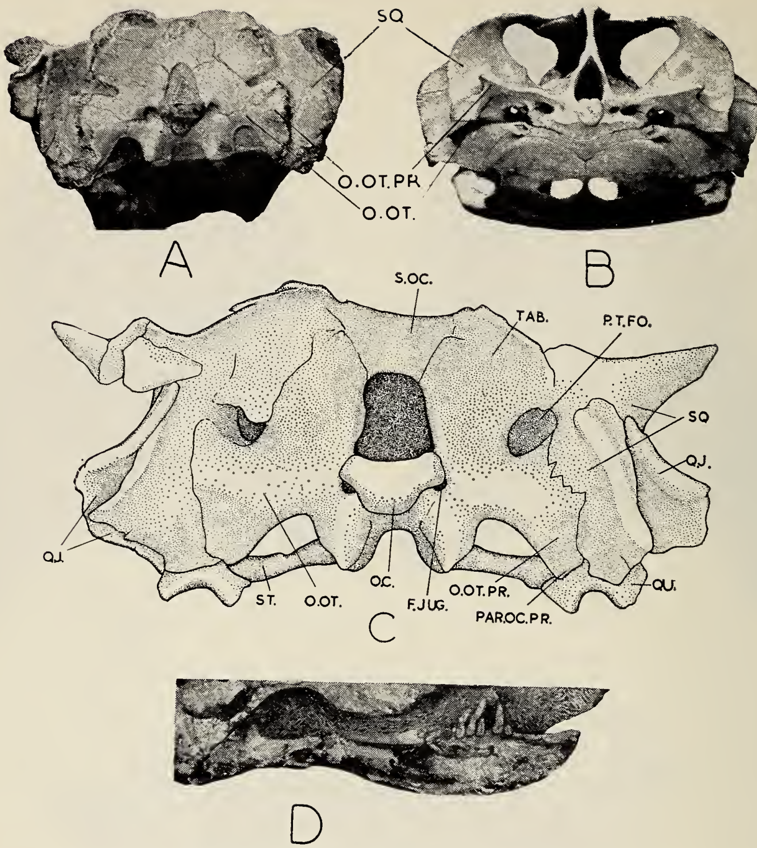
Abbreviations

A.C.I.	Arteria carotis interna.
ANG.	Angular.
ART.	Articular.
ART. FAC.	Arteria facialis.
A. OPHTH.	Arteria ophthalmica.
AS. R. EPT.	Ascending ramus of the epipterygoid.
A.V.S.C.	Antero-ventral semicircular canal.
B.	Bulge.
B.HY.	Basihyal.
B. OC.	Basioccipital.
B. PT. PR.	Basipterygoid process.
B. SPH.	Basisphenoid.

C.	Canine tusk.
CAL. C.	Calcified cartilage.
C.C.	Crus commune.
CR. SEL.	Crista sellaris.
DEN.	Dentary.
EC. PT.	Ectopterygoid.
E.N.	External naris.
EPT.	Epipterygoid.
Exocc.	Exoccipital.
F.BA.P.	Fenestra basicranialis posterior.
F. HY.	Fenestra hypophyseos.
F. JUG.	Foramen jugulare.
FL. FO.	Floccular fossa.
F. OV.	Fenestra ovalis.
F. PL.	Footplate of the stapes.
G.R.M.C.	Groove for Meckel's cartilage.
I.A.M.	Internal auditory meatus.
IN. PRO.	Incisura prootica.
I. PAR.	Interparietal.
I. PT. V.	Interpterygoidal vacuity.
JUG.	Jugular.
LAC.	Lachrymal.
LAT. FL. ANG.	Lateral flange of the surangular.
L.C.QU.	Lateral condyle of the quadrate.
L.G.	Longitudinal groove on the quadrate.
L.J.T.	Lower jaw teeth.
L.W. PARA.	Lateral wing of the parasphenoid.
M.C.QU.	Median condyle of the quadrate.
M.F.S. ANG.	Medial flange of the surangular.
MX.	Maxillary.
MX. ANT.	Maxillary antrum.
NAS.	Nasal.
N. LAC. F.	Naso-lachrymal foramen.
O.C.	Occipital condyle.
O. OT.	Opisthotic.
O. OT. PR.	Opisthotic process.
ORB. SPH.	Orbitosphenoid.
OS. TRAB.	Ossified trabeculae.
P. ART.	Prearticular.
PAL.	Palatine.
PAR.	Parietal.
PAR. OC. PR.	Paroccipital process of the opisthotic.
P.B. SPH.	Parabasisphenoid.
P. FOR.	Pineal foramen.
PL. SPH.	Pleurosphenoid.
P. MX.	Premaxillary.
PO. C.	Postcanines.
PO. FR.	Postfrontal.
PO. O.	Postorbital.
PR. FR.	Prefrontal.
PR. OT.	Prootic.
PR. PAR.	Preparietal.
P. SPH.	Parasphenoid.
PT.	Pterygoid.
P.T.FO.	Posttemporal fossa.
P.V.S.C.	Postero-ventral semicircular canal.
Q.J.	Quadratojugal.
Q.R. EPT.	Quadrate ramus of the epipterygoid.
Q.R. PT.	Quadrate ramus of the pterygoid.
QU.	Quadrate.
REF. LAM.	Reflected lamina of the angular.
RET. ART. PR.	Retro-articular process.
S. ANG.	Surangular.
S.C. REC.	Sacculo-cochlear recess.
SIN. UT.	Sinus utricularis.
S. MX.	Septomaxillary.
S. OC.	Supra-occipital.
SPL.	Splenial.
S.Q.	Squamosal.
S. SPH.	Septosphenoid.
ST.	Stapes.
ST. ATT.	Stapes attachment.
TAB.	Tabular.
TRAB.	Trabeculae.
VO.	Vomer.



Pristerodon buffaloensis. Type specimen. A: dorsal; B: ventral, and C: lateral view of skull.



A: occipital view of type specimen of *Pristerodon buffaloensis*; B: occipital view of *Phrynops* sp.; C: occipital view of sectioned specimen of *Pristerodon buffaloensis*; D: medial view of left half of lower jaw of type specimen of *Pristerodon buffaloensis*. Abbreviations on p. 160.

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In duplicate (one set of illustrations), type-written, double spaced with good margins, including TABLE OF CONTENTS and SUMMARY. Position of text-figures and tables must be indicated.

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SYNONYMY

Arranged according to chronology of names. Published scientific names by which a species has been previously designated (subsequent to 1758) are listed in chronological order, with abbreviated bibliographic references to descriptions or citations following in chronological order after each name. Full references must be given at the end of the paper. Articles and recommendations of the *International code of zoological nomenclature adopted by the XV International congress of zoology, London, July* 1958, are to be observed (particularly articles 22 and 51).

Examples: *Plonia capensis* Smith, 1954: 86, pl. 27, fig. 3. Green, 1955: 23, fig. 2.

When transferred to another genus:
Euplonia capensis (Smith) Brown, 1955: 259.
When misidentified as another species:
Plonia natalensis (*non* West), Jones, 1956: 18.
When another species has been called by the same name:
[*non*] *Plonia capensis*: Jones, 1957: 27 (= *natalensis* West).